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# Courtship Behavior in Linsleya compressicornis and its Taxonomic Significance<sup>1</sup>

(Coleoptera: Meloidae)

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The systematic position of the small, western North American genus Linsleya MacSwain has been the subject of recent controversy. Although members of this group were originally placed in Lytta on the basis of superficial adult resemblance (Horn, 1873), larval anatomy has now convinced most workers that they belong near Epicauta and Pleuropompha in the Epicautina (MacSwain, 1951, 1956; Selander, 1955, 1964a; Arnett, 1960; Werner, Enns and Parker, 1966). Yet, other authors (Kaszab, 1959; Gupta, 1965) continue to treat *Linsleya* as allied to Lytta. This study of courtship behavior was undertaken to provide additional information bearing on this question. Courtship in Linsleya (Linsleya) convexa (LeConte) was studied previously but failed to indicate subtribal affinity (Selander and Pinto, 1967). The behavior of a second species, L. (Linsleyina) compressicornis (Horn), is described below. This species is of considerable interest since its courtship is remarkably similar to that of several species of Epicautina and unlike any behavior known in the Lyttina<sup>2</sup>.

Adults utilized in this study consisted of 30 males and 28 females collected from their host plant, *Menodora spinescens* Gray (Oleaceae), 2 miles E of Big Pine, Inyo County, California, on 9 June 1973. Sexual isolation was effected 12 hrs after collection and was maintained whenever observations were not in progress. All observations were made in the laboratory from 12–20 June 1973, at 26–30°C. Specimens were maintained and observed in plastic cages 11½ cm long and 8 cm wide.

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<sup>&</sup>lt;sup>2</sup> This paper follows Selander's (1964b) classification in treating the Lyttina and Epicautina as subtribes within the Lyttini. Other authors (e.g. MacSwain, 1956) give these two taxa tribal status.

Ethological data are based on six hours of observation utilizing numerous randomly selected pairs, and include 200 feet of motion picture films.

L. compressicornis has been divided into two subspecies by Selander (1955). This study is based on members of the nominate form.

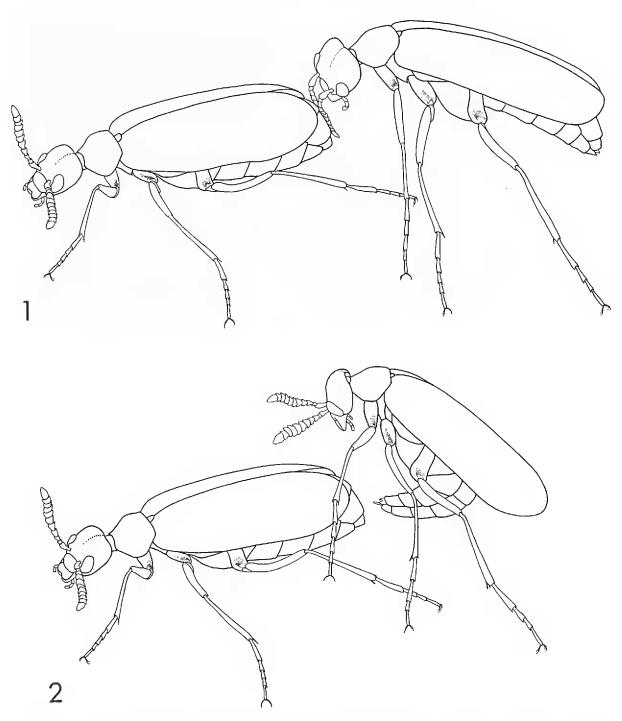
#### COURTSHIP BEHAVIOR

All components of courtship in *L. compressicornis* are performed by the male while positioned behind the female (posterior position). At no time does he mount her, or overtly contact her with his legs in any other way. For descriptive purposes courtship is divided into three phases, a preliminary phase, a display phase, and a genital phase.

At the onset of the preliminary phase the male orients directly behind a quiescent female. His maxillary palpi are often extended and irregularly touch the female's pygidium. The position and state of the male's antennae vary. They may be held motionless and out to the side or, more frequently, with segments II—XI directed downward at an approximate right angle to segment I and the anterior surface of each antenna facing the side of the female's last abdominal segment. While in the latter position the antennae are often rapidly vibrated anteroposteriorly. Periods of vibration vary in duration from one to 20 sec and comprise, on the average, 50–60% of total courtship time. Antennal vibration is usually repeated several times before the start of the display phase. Due to decamping by the female, however, some bouts never progress beyond preliminary phase activity.

Although antennal vibration is the dominant component of courtship in terms of time, its significance is not clear. Contact with the female apparently never occurs. Because of this and the lack of an obviously correlated female response, I have excluded this act from the display phase.

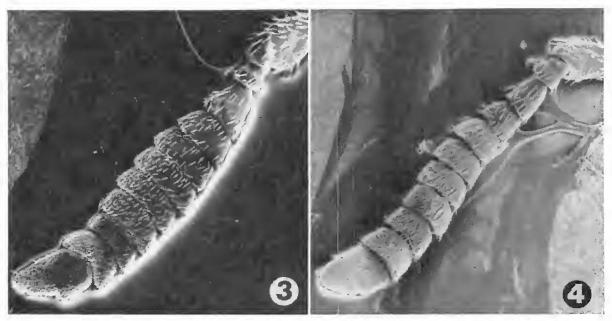
Display in L. compressicornis consists of a single act, antennal pressing (Fig. 1). This act is always preceded by antennal vibration. Prior to pressing the antennae are rotated so that their anterior surface is directed forward and, at the same time, they are moved slightly posteromedially to a position above the midline of the female's abdomen. Tactual stimulation immediately follows and consists of the male pressing down on the last two abdominal tergites of the female one to five times in rapid succession. Both antennae are employed synchronously with the anterior surface of segments IV–XI making contact. A determination of the number of presses normally provided during each bout of display is complicated by female activity. Most females thwart courting males



Figs. 1-2. Courtship behavior in *L. compressicornis*. Fig. 1. Display phase. Male performing antennal pressing. Fig. 2. Genital phase. Male attempting genital insertion.

by either decamping, kicking, or abruptly elevating their abdomen at the onset of display. The majority of bouts, however, consist of three presses. Display was not common in this study. It occurred, on the average, only once during every four minutes of courtship.

Display is invariably followed by a *genital insertion attempt* (genital phase) (Fig. 2). In attempting insertion the male maintains his posterior position, elevates his fore legs and, with genitalia partially extruded, curls the apex of his abdomen forward through his middle and



Figs. 3-4. Scanning electron micrographs of right antenna of L. compressicornis (anterior view). Fig. 3. Male  $(60\times)$ . Fig. 4. Female  $(50\times)$ .

hind legs toward the gonopore of the female. If, as is usually the case, the female does not allow mating, he either returns to preliminary phase activity or ceases courting entirely. Genital insertion attempts only occur after display. In my observations their duration varied from seven to 45 seconds.

The display and genital phases appear to be tied behaviorally in this species since insertion is always attempted immediately after pressing. This is even true when the female decamps during display. In this case the male quickly pursues the female and upon continuing courtship several seconds later resumes with an insertion attempt. Situations where the female successfully eludes the male were not observed.

Only a single mating was observed. This particular male inserted immediately after display, and within less than five seconds turned to his right and assumed the linear position without contacting the female with his fore legs. The duration of this mating was not recorded.

#### Anatomical Correlates of Courtship

Antennal modifications in the male of *L. compressicornis* are the most obvious correlates of courtship. As shown in Figs. 3 and 4, segments III—XI of the male are more strongly broadened than those of the female, and their anterior surface is concave rather than convex. Additional modification is found in antennal surface structure. Most of the male's segments have fewer setae on the anterior (contacting) surface, and segment XI is entirely denuded at its base. Examination of this surface at high magnification with the scanning electron microscope re-

veals an abundance of minute cuticular pores. These are especially dense at the base of segment XI, the area of greatest density appearing as a small ellipse at 60× (Fig. 3). The function of these pores is unknown. Their association with chemical stimuli has been suggested for other meloines (Matthes, 1969; Pinto, 1973).

Another modification in males of *L. compressicornis* is the highly developed fore tarsal pads. The pale, apically flared setae which comprise the pads in this species are best developed on the first three segments. In *Linsleya convexa*, similarly modified fore tarsal pads in the male are considered an adaptation for grasping the female while he is mounted on her (Selander and Pinto, 1967). In *L. compressicornis*, however, the male does not contact the female with his legs. Instead, the pads may aid the peripatetic males in maneuvering on the host plant surface during their persistent search for females and during courtship.

#### COMPARATIVE BEHAVIOR AND DISCUSSION

L. convexa is the only other species of Linsleya for which courtship data are available. This species shares few similarities with L. compressicornis besides traits typical of meloines in general<sup>3</sup>. In L. convexa the male courts entirely from a fully mounted position (dorsal position), and display consists of rubbing the dorsum of the female with his hind two pair of tarsi (Selander and Pinto, 1967). The only noteworthy similarity is that males of both species fail to manipulate the antennae of the female but stimulate her dorsum instead.

Courtship in L. compressicornis is remarkably similar to that of Pleuropompha and certain species of Epicauta. In both species of Pleuropompha and in Epicauta (Epicauta) puncticollis Mannerheim (Pinto, 1973), and in E. (Epicauta) ruidosana Fall (Pinto, unpubl.) the male also courts entirely from an unmounted posterior position. The genital phase is performed in the same manner in all five species, and although the specifics of display vary, employment of the antennae by the male is characteristic of all but E. ruidosana. In all other nominate Epicauta studied, the genital phase and often the display phase as well are performed from a dorsally mounted position (Pinto, 1973). A dorsal mount, at least during part of courtship, is typical of Meloinae. Its complete absence has been reported only in the above-mentioned species.

The act of antennal pressing in L. compressicornis is roughly similar to display in some other species of nominate Epicauta, namely E. pardalis LeC., E. magnomaculata Martin, and E. ventralis Werner (Pinto,

<sup>&</sup>lt;sup>3</sup> Courtship traits typical to the Meloinae are discussed by Selander (1964b).

MS). In these three species the posteriorly positioned male rubs or presses the dorsum of the female with his antennae. The specifics of this act in these *Epicauta* are sufficiently different, however, as to preclude homology with antennal pressing. As in both species of *Linsleya*, display in all nominate *Epicauta* that have been studied involves the stimulation of the female's dorsum in some way (Pinto, 1973), and is never directed toward her antennae. Antennal manipulation is found in most other meloine taxa (Selander, 1964b; Pinto, 1972) including *Epicauta* subgenus *Macrobasis* (Selander and Mathieu, 1969).

With respect to courtship then, *L. compressicornis* and certain species of nominate *Epicauta* are more similar to each other than to congeners. Unfortunately, we can not yet speculate knowledgeably as to whether posterior courtship, their shared pattern, represents the primitive or derived state in the Epicautina. However, it is clear that either posterior or dorsal courtship has been derived independently in the subtribe since the two patterns occur in both *Linsleya* and *Epicauta*. Such marked interspecific variation in the position of the courting male is surprising considering its constancy in other meloines. In other taxa (e.g. *Meloe*, *Lytta*, *Eupompha*, *Pyrota*) dorsal mounting is typical, and the position assumed by the male varies only slightly between species. The adaptive significance of posterior versus dorsal courtship can not be profitably discussed without analyses of several aspects of reproductive behavior and related ecological factors.

The similarities of behavior in *L. compressicornis* and certain *Epicauta* are marked. To the contrary, there are no important parallels to courtship in any lyttine studied so far. In species of *Lytta* the male invariably courts from a fully mounted position, and display, when present, involves the manipulation of the female's antennae (Selander, 1960; Matthes, 1972; Gerber and Church, 1973; Pinto, unpubl.). A similar pattern has been reported for the lyttine genus *Lydus* (Cros, 1912).

#### Conclusion

In spite of the failure of adult anatomy to clearly indicate relationship, both larval and ethological features can now be cited in support of placing the five species of *Linsleya* in the Epicautina. The similarities of the first instar larvae of *Linsleya*, *Epicauta* and *Pleuropompha* are numerous (see MacSwain, 1956) and, in themselves, leave little doubt as to the affinity of these genera. Selander (1964a) has also pointed out that larvae of *Linsleya sphaericollis* (Say) appear to be parasitoids of grasshopper egg pods (as in *Epicauta*) rather than of bee nests (as in

Lytta and related genera). The behavioral data presented above are of importance since they clearly support these conclusions based on larval anatomy and bionomics, and, furthermore, suggest that Linsleya is most similar to the nominate subgenus of Epicauta.

As mentioned above, Kaszab (1959) and Gupta (1965) continue to place Linsleya near Lytta<sup>4</sup>. Kaszab's rationale for this is not clear. Although his 1959 classification of the Meloidae is primarily based on wing venation, the wings of Linsleya are poor indicators of subtribal affinity as they are similar to those of both Epicauta and Lytta. Gupta's reassignment of Linsleya was prompted by the absence of two structures in L. sphaericollis, V-shaped proventricular folds and well developed stomadaeal valves. Both traits are present in Epicauta and Pleuropompha; other epicautine genera (Psalydolytta, Denierella and Anomalonchus) were not studied. To reassign Linsleya solely on this basis is not convincing. If Linsleya is the most primitive genus of epicautine as both MacSwain (1951) and Selander (1955) believe, its lacking certain specializations of the more derived genera should not be surprising.

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<sup>&</sup>lt;sup>4</sup> In a recent classificatory outline of the Meloidae, Kaszab (1969, Mem. Soc. Entomol. Ital., 48: 243) lists *Linsleya* as an epicautine.

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